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ANATOMICAL CHARACTERS IN THE EVOLUTION OF *PINUS*¹

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Pinus is the oldest genus of the conifers and the most important and interesting, whether considered from the botanical, economic or aborigicultural standpoint. Occurring as it does in many species throughout the whole northern hemisphere, from it are derived many of the most valuable timbers and extractable products of commerce. In accordance with the general impression, that flourishing genera are modern, since they show an obvious adaptation to existing conditions of environment, it has been assumed that *Pinus* is of comparatively recent origin and marks the last word as it were in coniferous development. Recent investigations however of the occurrence of *Pinus* in the American Cretaceous, show that in the lower levels of that epoch, species of pines were apparently much more numerous than they are at the present time. It is accordingly apparent that so ancient a genus as *Pinus* and one so richly endowed with an abundant modern progeny supplies a particularly favorable subject for evolutionary investigation.

It has been the practice in the past to arrange plants systematically on the basis of external characters alone, chiefly on the superficial features of their floral organs and leaves. In the case of so ancient a genus as that under consideration, this procedure has peculiar difficulties connected with it, since in the tremendous period of time during which it has been in existence, its external characters have undergone many puzzling changes. The internal structure of the genus however has shown

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 22.

less range of variability and greater constancy in definite lines. On account of the long geological range of *Pinus*, anatomical characters, notoriously more constant than any others found in the higher plants, have had time to become considerably diversified. As a result of the action of this principle, it is much more easy to differentiate two such *species* as *Pinus strobus* Linn. and *P. palustris* Mill. from one another anatomically than distinct Cupressineous *genera* such as *Chamaecyparis* and *Thuya*. This arises from the fact that the Cupressineæ, to which the two last-named genera belong, are of very recent origin compared with many of the species of *Pinus*.

Before attacking the anatomical differences which mark the main lines of evolution in pines, it will be well to consider the artificiality of the groups into which they may be divided by the use of solely superficial characters. Such characters are the number of leaves in the fascicle, the deciduous or nondeciduous nature of the leaf-sheath, the texture of the cone-scale and the relative size of the seeds. Quinate leaf fascicles formed, for example, a very satisfactory basis for the classification of pines before those of the southern United States and Mexico became known to science. In Europe, Asia and northern North America, the possession of quinate leaf fascicles is a constant character of soft pines of the *Strobus* and allied sections. In the southern region of North America, however, are found hard pines such as *P. Torreyana* Parry, *P. arizonica* Englm. and *P. Montezumæ* Lamb. with leaf fascicle containing five leaves. On the other hand, a *persistent* leaf sheath such as is a feature of the hard pines is absent in *P. chihuahuana*, *P. leiophylla* and *P. Lumholtzii*, quite typical pines of the group in other respects. Nor is the texture of the cone-scale or the position of the apophysis on the umbo, characters which are used to distinguish the larger groups of Pines, any less exempt from disconcerting exceptions. The American nut-pines, as well as those of

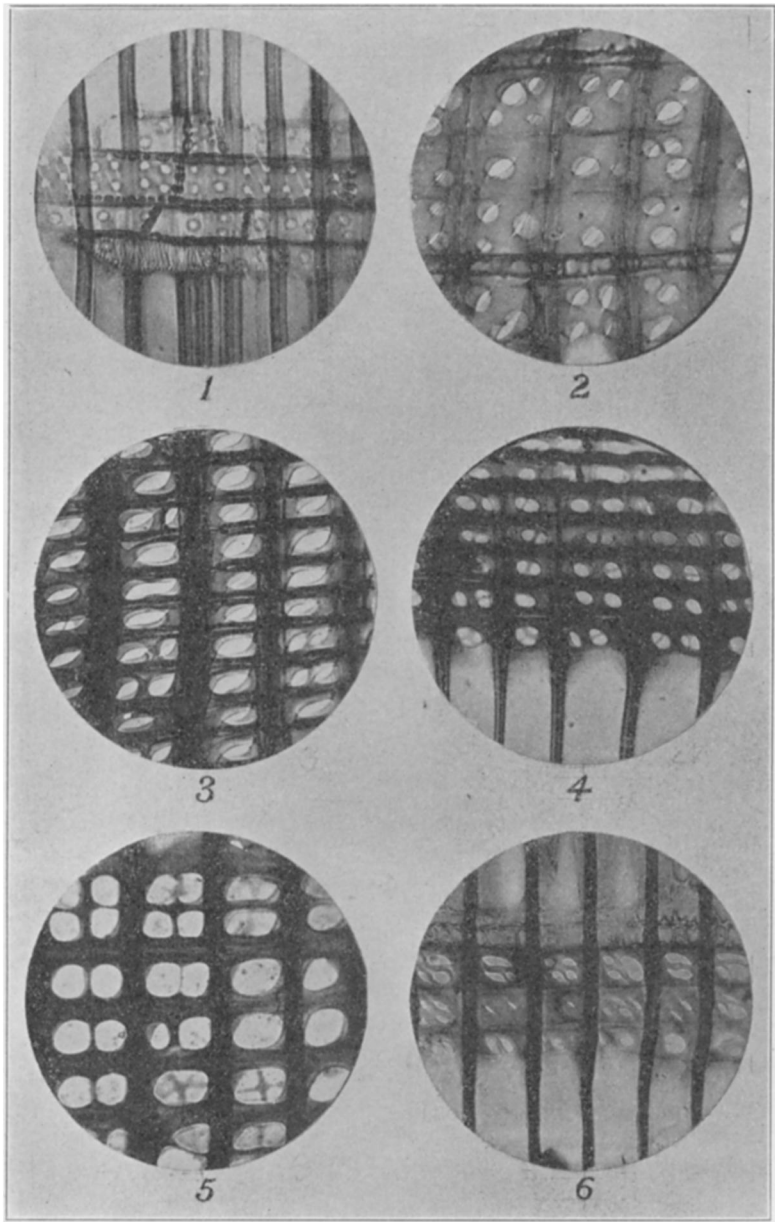
Asia, although belonging to the soft pine series have the thick cone-scales and median dorsal umbo of the hard pines. Nor is the nut-like character of the seed a constant character, for the nut-pine of Italy is a hard pine, while those of America and Asia are soft pines. If we seek for really dependable criteria for the classification of pines, we have to go below the surface. The single leaf-trace, for example, is absolutely constant throughout the soft-pine series as is equally the case with the double foliar bundle in the hard-pine series. Similarly, the soft pines are characterized by a single row of resin-canals in the first year's growth which is duplicated or further multiplied in the hard pines. Englemann has further indicated the value of the number and position of the resin canals in the leaf for diagnostic purposes. An extremely important anatomical character for the separation of the two great series of living pines is the nature of the tracheid-like cells on the margins of the wood-rays. The nature of the pitting in the tracheids of the wood and the central cells of the wood-rays likewise supply valuable criteria for the establishment of smaller subdivisions. It will be inferred from what has been said, that anatomical characteristics in the case of *Pinus* are very constant in broad lines and consequently are for the establishment of a natural classification, indicating the evolution of the genus, of the greatest value. External characters, on the other hand, are much subject to variability.

Two main series of pines, the hard pines and the soft pines, may be clearly recognized, in accordance with anatomical characters. For example, the groups of which *P. strobus* Linn. and *P. silvestris* Linn. are types, are quite distinct. The latter species is characterized with the remaining hard pines, without exception, by the double foliar fibrovascular bundle, two or more rows of resin canals in the first ring of woody growth and dentate or reticulate marginal tracheids of the wood-rays. The former species, together with the other soft pines,

has throughout the single leaf bundle, the single row of resin canals in the first woody ring and smooth-walled marginal ray-tracheids.¹ These two great races of pines, which may be traced from the Cretaceous to the present, may be subdivided on the basis of other characters, internal and external. Within the subdivisions differences in floral and foliar characters are much less variable than in the main lines.

The nature of the parenchyma in the wood rays and the characters of the pits which connect them with the tracheids are features of considerable evolutionary and diagnostic importance in the various smaller subdivisions of the genus under consideration. For example, among the soft pines we find a group illustrated by the nut pines and foxtail pines of the United States, and by the nut pines of Asia (*P. Gerardiana* Wallich. and *P. Bungeana* Zucc.), which are characterized by the possession of thick-walled ray parenchyma, with very small lateral pits having distinctly circular borders (Fig. 1). These pits are usually four in each "cross field" (a cross field is the area of intersection of a ray cell and a tracheid) and quite distinctly separated from each other. The opening on the side of the tracheid is slit-like and often exceeds in length the diameter of the pit. The opening on the side of the ray cell is circular or lenticular and smaller or nearly equal in diameter to the border. In most of the nut pines and fox-tail pines these pits are rather uniform in size and in diameter, the same as the lateral pit in the marginal tracheids of the rays. In *P. Bungeana* of China the pits are of large size, with widely lenticular openings and more approximated than in the other nut pines. Small lateral pits such as those just described with distinct circular borders are characteristic of the ray cells of most of the conifers and are conveniently termed "piciform."

¹ Smooth-walled except for occasional spiral markings (see Fig. 1) which are quite distinct from the heavily sculptured reticulate and dentate marginal tracheids of the hard pines.



EXPLANATION OF PLATE

FIG. 1. Radial section of *Pinus Balfouriana*, showing the thick-walled character of the ray parenchyma, the characteristic piciform pitting of the nut pines, and a *ray tracheid with spiral markings* which are characteristic of this species. $\times 500$.

FIG. 2. Radial section of the root of *Pinus taeda*, showing the variation in the size of the pits, the distinctly bordered outlines and the increase in width of the orifice with increase in size of the border. $\times 300$.

FIG. 3. Radial section of *Pinus Ayacahuite*, showing large pits with distinct circular borders and their fusion in places into large pits with oblong borders. $\times 300$.

FIG. 4. Radial section of *Pinus Lambertiana*, showing the formation of one or two medium-sized pits by the fusion of 2-4 small pits. The fusion has progressed most rapidly on the tracheid side and the ghost-like remains of the parenchyma partitions may still be seen. $\times 200$.

FIG. 5. Radial section of *Pinus flexilis* James, showing on the upper side the process by which four medium-sized pits, produced by fusion, are fusing in turn into one or two medium-sized pits. In the center two medium-sized pits are fusing into a single large pit, and at the bottom two pits, in which the tracheid wall has fallen away before the parenchyma wall, may be seen. The ghost-like remains of the divisions of four and five small pits are still visible. $\times 300$.

FIG. 6. Radial section of *Pinus palustris*, showing piciform pits, the increase in size of these, and their fusion into irregularly shaped pits of many forms. $\times 500$.

In the majority of the hard pines of the United States, we find ray pits somewhat similar to those of the nut pines. There are present one to eight small pits in each cross-field (Fig. 2). These pits, however, are very variable in size, number, form and structure. In some species, and in certain regions in almost all species, small piciform pits may be found (Fig. 6) occurring with these. In most species are pits with circular borders of larger size and wide slit-like or lenticular orifices (Figs. 2 and 6). In places these pits become approximated and the borders fuse to form a single irregular border surrounding an elongated irregular pit. In certain species such as *P. palustris* Mill., *P. Murrayana* A. Murray, *P. taeda* Linn., etc., numerous pits of large size may originate in this way. These are often crescentic, long oval, sausage-shaped or widely lenticular in form (Fig. 6). In hard pines we see two distinct lines of specialization in the formation of large pits, a tendency for the piciform pits to simply increase in size or a tendency for pits of large dimensions to be formed from the fusion of smaller ones. Hand in hand with the transition from small piciform to large pits there occurs a transition from thick to thin-walled ray parenchyma cells. Certain Pines (*e. g.*, *P. Murrayana* A. Murray) show all gradations from thick-walled cells such as are characteristic of nut pines to very thin-walled cells, such as occur in the rays of *P. strobus* Linn. It is of interest to note that pit fusions take place equally in both thick- and thin-walled ray elements. Either the thick- or thin-walled type of cell may predominate in the ray of the various hard pines. In the seedling and the woody axis of the cone of such pines, we find the ancestral piciform type of pitting well represented, and in the cone-axis in particular the ray parenchyma is thick walled.

In both the hard and soft pines there is a group characterized by the possession of one or two very large pits in each cross-field (Figs. 3 and 5). In places, however,

these may be represented by several small pits, and transitions may be found showing the development of these large pits from the smaller ones by fusion. In Fig. 5 is seen a condition characteristic of *P. strobus* Linn., *P. silvestris* Linn., *P. Laricio* Poir., *P. Thunbergii* Parl., *P. Koraiensis* Sieb. et Zucc., *P. resinosa* Sol., *P. Cembra* Linn. and other pines with large lateral ray pits. In the upper part of Fig. 5 the stages in the development of two large pits from four small ones may be made out, while in the central region appears the origin of a single large pit from two smaller ones. In the lower part of the same figure may be seen instances of multiple fusion, such as are particularly characteristic of the soft pines, where the pit openings on the side of the tracheids often fuse before those on the side of the ray, so that the ghost-like relic of the separating ray wall may still be observed. In Fig. 4 is seen a condition, which may be considered to illustrate the formation of pits of medium size in Fig. 5. One or two rather small pits are being formed in most cases from the fusion of from two to four very small piciform pits. In Fig. 3 is seen a condition characteristic of certain soft pines (*P. Avacuite* Ehrenberg, *P. albicaulis* Englm., etc.) where the large-bordered pits have formed and are fusing in places to form elongated pits with oval outlines. The large pitted soft and hard pines show in the seedling a reversion to the ancestral condition of numerous small pits and in their cone-axes piciform ray pits are characteristically present. Such pines have ordinarily thin-walled rays cells, with the exception of such intermediate species as *P. Lambertiana* Doug. and *P. Ayacuite* Ehrenb.

With this review of the ray pitting in modern pines, it will be apparent that in the nut and fox-tail pines we have exclusively piciform pitting in the lateral walls of the ray. This condition is of interest because it perpetuates the type of pitting which has been invariably found in the rays of Cretaceous pines as well as in

Prepinus Jeffrey, which must be regarded as a very antique representative of the pine-like conifers. This is particularly significant on account of the other ancestral features presented by the nut pines. In both the hard and soft pines of the present epoch we find a gradual transition from the thick-walled rays cells with abundant piciform pitting of the ancestral type to thin-walled cells with few large compound pits. These large pits have been formed for the most part by the fusion of smaller pits, although in some instances they appear to have been derived by the simple enlargement of the piciform type of pit. It is of interest to note that the succiniferous pines, which gave rise to the Baltic amber in the late Eocene or early Oligocene, already show the transition from the piciform to the large type of pit.¹ Conwentz notes that there may be from one to four pits in each cross-field and that the number decreases with the increase in size. He further notes that in certain regions the pits are predominantly small and in others large, but draws no conclusions as to the origin of the latter. From a consideration of the mode of formation of the large ray pits of *Pinus*, we see that the two main divisions of the genus fall roughly into two principal subgroups, one less specialized with one or several small pits in each cross-field of the wood ray and the other more highly specialized with large infrequent pits in thin-walled ray cells. These subgroups grade into one another, but by recourse to other features of anatomical specialization as well as to external characters, a satisfactory basis for further subdivision along true evolutionary lines is obtained.

SUMMARY AND CONCLUSIONS

1. By a study of the anatomy of fossil and living pines certain lines of descent may be somewhat clearly discerned.

2. Cretaceous pines as well as *Prepinus* Jeffrey were

¹ Conwentz, Monog. d. Balt. Bernsteinbaume, pp. 55-56, Tab. XIV, 7, Tab. X, 4.

characterized by thick-walled ray parenchyma and piceiform lateral ray pits, by the absence of marginal ray tracheids and by abundant tangential pitting of the autumnal tracheids.

3. The development of ray-tracheids, the disappearance of thick-walled ray cells, the origin of large compound ray pits and the loss of tangential pitting in the autumnal tracheids are all features of the evolutionary development of the pines of the present epoch.

4. The large lateral pits of the rays in modern species of *Pinus* have taken their origin for the most part by the fusion of small pits with distinct circular borders.

5. The hard and soft pines with very large lateral ray pits are the most highly developed living pines. The type of hard pines represented by *P. resinosa* in North America and *P. silvestris* in Europe, represent in the concurrent development of very large generally solitary lateral ray pits, with dentate marginal ray tracheids and the obliteration of tangential pitting in the autumnal tracheids, except in the seedling and in the woody axis of the cone, the most highly developed and specialized condition among living pines.

6. The nut pines of North America and Asia have piceiform lateral ray pits and thick-walled ray cells and in these features approach most nearly to the conditions of structure found in Cretaceous pines.

7. The hard pines of the United States, with the exception of *P. resinosa*, show a great range of variation from piceiform to compound lateral ray pits. The soft pines present a parallel series of gradation in ray pitting.

In conclusion, I wish to express my thanks to Professor Jeffrey for material of Cretaceous and other pines and for aid in securing the photomicrographs with which this article is illustrated. To Professor Jack I am indebted for specimens of the woods of Asiatic pines and to Mr. E. W. Sinnott for the opportunity of examining serial sections of the seedlings and cone-axes of a number of pines.